Chromosome races in *Sarcobatus* (Sarcobataceae, Caryophyllales)

Stewart C. Sanderson  
*Shrub Science Laboratory, Rocky Mountain Research Station, Forest Service, U.S. Department of Agriculture, Provo, Utah*

Howard C. Stutz  
*Brigham Young University*

Mildred Stutz  
*Brigham Young University*

Richard C. Roos  
*Waste Management Federal Services, Inc., Northwest Operations, Richland, Washington*

Follow this and additional works at: https://scholarsarchive.byu.edu/gbn

Recommended Citation  
Available at: https://scholarsarchive.byu.edu/gbn/vol59/iss4/1
CHROMOSOME RACES IN SARCOBATUS
(SARCOBATACEAE, CARYOPHYLLALES)

Stewart C. Sanderson1, Howard C. Stutz2, Mildred Stutz2, and Richard C. Roos3

ABSTRACT.—Sarcobatus Nees., a genus of North American halophytic shrubs, consists of 2 species: S. verniculatus (Hook.) Torr. \((n = 18, 36)\), which is widespread in western North America, and S. baileyi Cov. \((n = 54)\), endemic to Nevada. Within S. verniculatus, populations of \(n = 36\) are widely distributed, whereas populations of \(n = 18\) are found only in the Sonoran Desert, northern California, and northwestern Great Plains, locations at the periphery of the species range. Although the chromosome number of \(n = 18\) is apparently tetraploid, failure to form an \(n = 27\) race intermediate to those of \(n = 18\) and \(n = 36\) suggests that \(n = 18\) S. verniculatus is of significant age and that it behaves chromosomally as a diploid. Sarcobatus has a long fossil pollen record and endured Pleistocene climatic extremes with little range displacement.

Key words: Sarcobatus, polyploidy, autopolyploidy, diploidization, Pleistocene distributions.

Sarcobatus Nees. is an endemic North American genus consisting of spiny shrubs that are monoecious and wind-pollinated, with reduced, fleshy leaves. It has historically been placed in the Chenopodiaceae (order Caryophyllales). Like members of subfamily Salsoloideae (Spiralobae) in the Chenopodiaceae, the embryo of Sarcobatus is elongate and coiled in seed, enabling rapid extension during germination. In common with the chenopod genera Spinacia, Atriplex, and Ceratoides, plants of Sarcobatus contain 6-oxygenated flavonoids (Sanderson et al. 1988). Of 12-plus families in the Caryophyllales, 6-oxygenated flavonoids are otherwise known to date only from the Amaranthaceae and Aizoaceae (Rodman 1994). Sarcobatus propagules, formed from the winged calyx of female flowers, are adapted for wind dispersal across barren surfaces such as mud flats or sand dunes (Danin 1996). The segments of this calyx are accrescent and enclose the seed in fruit (Standley 1916, Welsh et al. 1993), somewhat like that of some chenopods.

In spite of these similarities to the Chenopodiaceae, other Sarcobatus characteristics are discordant within that family. Macromolecular and sieve-tube plastid evidence suggests a linkage of the genus to other families, particularly

1 Shrub Sciences Laboratory, Rocky Mountain Research Station, Fort Collins, U.S. Department of Agriculture, 735 N. 500 East, Provo, UT 84606. Author to whom requests for reprint should be sent.
2 Department of Botany andRange Science, Brigham Young University, Provo, UT 84602.

A feature of Sarcobatus not duplicated in any related family is the male inflorescence in which numerous, asepalous flowers are borne in a conelike structure formed from peltate scales. In view of the distinctiveness of Sarcobatus, a separate family, Sarcobataceae, has recently been created for it (Behnke 1997).

Fossil pollen of Sarcobatus has been found in Eocene, Oligocene, and later strata from localities in Washington, Oregon, Idaho, Wyoming, and Colorado (Leopold and Maginnis 1972, Leopold and Denton 1987); the genus was present in late Miocene in the area of Jackson Hole, Wyoming, before the present Teton Mountains were uplifted (Barnosky 1984). Because floras during the early and mid-Tertiary were considerably more tropical and preponderantly arboreal (Leopold and Maginnis 1972), Sarcobatus may have had somewhat different environmental tolerances at that time than it does at present. However, it would likely have grown on the margins of desert lakes rather than within forests.

Sarcobatus at present consists of 2 species, S. vermiculatus (Hook.) Torr., of wide distribution in western North America, and S. baileyi Cov., which is limited to the central and western parts of Nevada in the Great Basin. Sarcobatus vermiculatus occupies saline bottomlands, playas, dunes, and badlands, while S. baileyi is found on arid slopes, usually in monotypic stands or in association with Atriplex confertifolia.

The only published chromosome count for Sarcobatus of which we are aware is n = 18, from a collection of S. vermiculatus near Medicine Hat, Alberta (Bassett and Crompton 1970). The Chenopodiaceae and Phytolaccaceae have base chromosome numbers of x = 9 (Turner 1994). Although the Nyctaginaceae has a variety of chromosome numbers, Turner (1994) suggests its base may be x = 10. Nevertheless, x = 9 would be a plausible alternative. Sarcobatus is somewhat isolated phylogenetically, but it seems likely, in view of its relationships with these families, that x = 9 is its base number as well.

It is our purpose to report on the distribution and morphological characteristics of the chromosomal races we have encountered within taxa of the new family Sarcobataceae, and to present available evidence regarding their origin and genetics.

**MATERIALS AND METHODS**

Chromosome counts, leaf-flavonoid content, and morphological measurements of Sarcobatus were obtained from sites throughout its range, and representative voucher specimens have been deposited at BRY. Cytological and chemical methods have evolved somewhat during accumulation of data for this report (1982–1996). The following procedures are currently used.

**Chromosome Counts**

We have found the use of 5% acetic acid or an equivalent strength of household vinegar to be safer for field use and to give results comparable to those of alcohol-acetic acid in fixation of meiotic material for taxa of the Chenopodiaceae and Sarcobatus (Stutz and Sanderson 1983, Sanderson and Stutz 1994). We determined chromosome counts from pollen mother cells of male flower buds fixed in vinegar (5% acetic acid strength) and refrigerated (2°C) or frozen (–20°C) for up to several months before examination. Anthers were squashed in acetocarmine stain, which was concentrated to supersaturation by means of evaporation on the microscope slide. Preparations were preserved by replacement of the dye solution under the cover slip with 45% acetic acid, and then with corn syrup, thinned as necessary with vinegar, which retarded mold growth in the syrup solution better than did 5% acetic acid. A few additional counts were made from root tips using methods described by Stutz and Sanderson (1983).

**Flavonoids**

Determination of aglycone moieties of foliar flavonoids was carried out upon either 25 cc of crushed air-dried leaves or a similar volume of 5% acetic acid–preserved leaf material. Samples were hydrolyzed for 60 min in 1N HCl over a boiling water bath to remove glycosidic sugars, then ground in 85% aqueous methanol, filtered, and washed with additional 85% methanol. The combined filtrate and washings (50 mL total) were mixed with an equal amount of water and then extracted with 50 mL of ethyl acetate, and again afterwards with a small rinse. The combined ethyl acetate extract and rinse was blown down with compressed air and the residue extracted with 1–2 mL 45% acetic acid, which was then applied to half-
sheets of Whatman 3M chromatography paper. Chromatography was carried out as reported previously (Sanderson and Stutz 1994), and sheets were thoroughly air- or oven-dried between 1st- and 2nd-dimensional chromatography. Most flavonoid compounds occurring in Sarcobatus have been previously isolated and chemically identified (Sanderson et al. 1988).

Morphology

Morphological characteristics of mature Sarcobatus plants in natural populations were measured in late summer 1995. Measurements were pooled from 5 plants in each population and compared statistically by taxon, ploidy, and geographic area using ANOVA (Proc GLM) and the Studentized Maximum Modulus (GT2) means comparison test for unequal sample sizes (SAS Institute 1989). Characteristics measured were plant height and width, leaf length and width (measured from a large leaf on the branch nearest the investigator), and male inflorescence length (excluding peduncle). Male inflorescence width could not be included because inflorescences in S. baileyi had already shed most of their scales at the season in which measurements were taken.

RESULTS

Original chromosome counts representing 224 localities (Fig. 1, Appendix) were obtained in this study. Sarcobatus chromosomes are small, but large enough for figure-8 bivalents to occur at a moderate frequency (Fig. 2). Meiosis appeared to be regular in both diploid \((n = 18)\) and octoploid \((n = 36)\) S. vermiculatus plants as well as in 12-ploid \((n = 54)\) S. baileyi. Abnormalities such as multivalents were observed only rarely, and spontaneous increase to higher ploidy appears to be relatively rare.

Except where there was geographic overlap of races of different ploidy levels, populations containing individuals of a higher ploidy occurred in only a few cases (Appendix). In 2 of 166 apparently octoploid populations of S. vermiculatus that were sampled, a single 12-ploid individual was also encountered. One population was located northwest of Tonopah, Nevada, and the other near Willard, New Mexico. Individuals of intermediate chromosome numbers of approximately 9-ploid to 10-ploid, apparently representing backcrosses of 12-ploid individuals to parental octoploid plants, were encountered in 6 additional instances. However, no plants of higher chromosome numbers were identified within populations of tetraploid S. vermiculatus, nor in S. baileyi.

Octoploid populations of S. vermiculatus were found to occupy the majority of the species range, from Montana and the Dakotas to northern Arizona, and from Colorado and Nebraska westward to California (Fig. 1). Tetraploids were limited in the north to Alberta, Saskatchewan, northern Montana, and North Dakota; in the west they occurred in Mono and Modoc counties of eastern California.

In a somewhat different ecological setting at the southernmost part of the species range, extensive populations of S. vermiculatus have been reported in the Gran Desierto of northern Sonora (Ezcurra et al. 1988), growing in coastal areas with shallow water tables, upon partially stabilized sand dunes and at the edge of salt pans. Our samples showed that these plants are tetraploid. A few small populations of similar tetraploid plants are found near the Gila River in southern Arizona, growing on sandy sites in areas unmodified by agriculture. Except for the Sonoran Desert plants and a few rare octoploids at northern extremes or higher elevations, Sarcobatus is otherwise absent from the Chihuahuan, Sonoran, and Mojave warm deserts of the southwestern United States and Mexico.

Tetraploid and octoploid populations growing in close proximity were encountered in the upper Pit River drainage, at Goose Lake on the California-Oregon border, and at sites in Montana and North Dakota (Fig. 1, Appendix). In a mixed-ploidy site near Goose Lake, west of Davis Creek, California, chromosome counts of 17 plants showed that, although in close proximity, the tetraploid and octoploid plants formed discrete patches (Fig. 3). While all were browsed severely by cattle at that site, those in the octoploid patch appeared taller and more vigorous, as contrasted with the smaller, more heavily damaged plants in the tetraploid patches. We found no plants at any of the mixed-ploidy sites with intermediate chromosome numbers suggestive of interploid hybridization.

Because individuals of S. vermiculatus show considerable vegetative plasticity, it is often difficult to distinguish tetraploid from octoploid plants in the field. However, as shown in
Table 1, the leaves of tetraploid plants are statistically shorter and narrower than those of octoploids.

Populations of octoploid *S. vermiculatus* may differ dramatically in stature (Roos 1984; Figs. 4, 5, Table 1), differences which are largely maintained in the common garden (Stutz unpublished data). However, only slight variation was encountered across larger geographical ranges. Plants from northern Oregon and Washington (the "northwestern Sx" group) were numerically tallest, though this was not statistically significant.

Inflorescence length showed few differences between ploidy or by geographic region in *S. vermiculatus*. However, temporal variation was observed which at a particular season gave the impression of geographic differences (data not
Since we observed many populations both in early summer when meiotic buds were being collected, and later at the time when morphological measurements were taken, it was possible to compare inflorescences produced at these different times and observe differences that may have resulted from changes in season or weather. In early summer 1995, inflorescences of octoploid populations in northern California were very short compared to those observed elsewhere. However, as shown in Table 1, by late summer, at the time when measurements were taken, inflorescences were as long as or longer than those of other areas. Also, male inflorescences in some octoploid populations of northern Arizona and southern Utah were observed to be of normal size in early summer, but by measurement time were shorter (and much less abundant) than those of northern populations.

Male inflorescences of *S. baileyi* plants are consistently shorter than the shortest lengths of those of *S. vermiculatus* (Table 1). This was observed to be true both for young inflorescences, in which pollen mother cells were undergoing meiosis, and also in mature inflorescences after pollen had been shed. The plants of *S. baileyi* are generally also shorter...
Table 1. Average of population means for Sarcobatus baileyi (SABA) and S. vermiculatus (SAVE) for morphological characters, measured in late summer, with standard error in parentheses. Column values within the same section that have a letter in common are not significantly different (SMM test).

<table>
<thead>
<tr>
<th></th>
<th>Plant</th>
<th>Leaf</th>
<th>Male inflorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. populations</td>
<td>Height (cm)</td>
<td>Width (cm)</td>
</tr>
<tr>
<td>S. baileyi</td>
<td>12x</td>
<td>5</td>
<td>53.7(3.83) b</td>
</tr>
<tr>
<td>Northern-4x</td>
<td>6</td>
<td>81.2(5.08) b</td>
<td>140.0(10.67) c</td>
</tr>
<tr>
<td>Northern-8x</td>
<td>10</td>
<td>106.6(23.21) ab</td>
<td>149.4(23.49) bc</td>
</tr>
<tr>
<td>Northwestern-8x</td>
<td>6</td>
<td>168.1(22.25) a</td>
<td>290.8(37.12) a</td>
</tr>
<tr>
<td>Central-8x</td>
<td>7</td>
<td>104.9(15.21) ab</td>
<td>187.6(32.08) a</td>
</tr>
<tr>
<td>Western-4x</td>
<td>5</td>
<td>134.2(9.68) ab</td>
<td>249.6(22.99) ab</td>
</tr>
<tr>
<td>Western-8x</td>
<td>11</td>
<td>121.8(4.89) ab</td>
<td>238.5(13.31) ab</td>
</tr>
<tr>
<td>Southern-4x</td>
<td>6</td>
<td>126.8(7.45) ab</td>
<td>215.1(17.41) abc</td>
</tr>
<tr>
<td>Southern-8x</td>
<td>5</td>
<td>103.2(22.06) ab</td>
<td>196.8(33.93) abc</td>
</tr>
<tr>
<td>SABA Total</td>
<td>3</td>
<td>53.7(3.83) b</td>
<td>133.3(33.51) a</td>
</tr>
<tr>
<td>SAVE Total</td>
<td>64</td>
<td>111.6(5.76) a</td>
<td>196.4(9.63) a</td>
</tr>
</tbody>
</table>

than those of octoploid S. vermiculatus, but are not significantly shorter than tetraploids using the present data set. Leaves of S. baileyi are shorter than those of either ploidy of S. vermiculatus, while not any narrower.

Although S. baileyi has been suspected to intergrade with S. vermiculatus (McMinn 1939), we found no morphological or cytological evidence for hybridization. S. baileyi was n = 54 throughout its range, but S. vermiculatus, even when growing nearby, was always n = 36. In locations where S. vermiculatus and S. baileyi come into contact, S. baileyi plants are often taller than usual, probably because of moister conditions, and conversely, S. vermiculatus plants become smaller and more spiny in drier circumstances, as they come near populations of S. baileyi. In spite of this convergence in stature, any confusion about their identity can be resolved when male inflorescences are present, and foliage characteristics are also often helpful. Besides the difference already noted in leaf length, leaves of S. baileyi are earlier-deciduous in the late summer than that of S. vermiculatus, and the time of appearance of new leaves in the spring usually differs, with S. baileyi leafing out first.

Sarcobatus baileyi flowers most profusely at leaf-flush, with male floral buds appearing terminally on new short shoots arising from the axils of woody branches. If conditions are favorable, a 2nd crop of inflorescences may be produced on the apices of elongate shoots. In S. vermiculatus, all flowering is on elongate shoots and may continue all summer when moisture is adequate (whether this relates to lowering of water tables through the season or to the exhaustion of surface moisture would be a matter for further study). Individual female flowers are usually located immediately below male inflorescences in both species.

As previously reported (Sanderson et al. 1988), the flavonoid complement of Sarcobatus species evidences the presence of an enzymatic activity for flavonol 6-oxygeuation, with individual plants showing some or all of the 6-methoxy flavonols (6-methoxy kampferol, patuletin, and spinacetin), as well as the corresponding 6-unsubstituted flavonols (kampferol, quercetin, and isorhamnetin). In addition, 3-O-methylated flavonols were often observed. S. baileyi plants from southeastern Nevada had flavonoids in proportions similar to those seen in S. vermiculatus, but samples from the western part of its range (western Nevada) showed a quantitatively different and more variable flavonoid profile, often with only small amounts of 6-methoxy compounds. We have not been able to discover morphological traits that correlate with this biochemical difference.
DISCUSSION
Late Pleistocene and Holocene Distribution Patterns

Changes in altitudinal or geographic range were widespread among plants of western North America in response to fluctuating climates during the Pleistocene and Holocene (Betancourt et al. 1990). However, because of its apparent limitation to saline soils, Sarcobatus may be an example of a taxon with a range that did not shift extensively during these time periods.

Although long-distance eastward transport of small amounts of Sarcobatus pollen has been noted (Maher 1964, Birks 1981), more abundant stratigraphic occurrences would indicate that the genus was present locally (Thompson 1992), especially in the western or upwind parts of its species range. The presence of Sarcobatus pollen at near-full glacial or earlier is documented by longer pollen records from the
Columbia Basin in Washington (Barnosky 1985), eastern Idaho (Beiswenger 1991), northwestern Wyoming (Whitlock 1993), central Nevada (Thompson 1992), Owens Valley, California (Koehler and Anderson 1994), and northern Arizona (Anderson 1993). In addition, pollen or macrofossil records document the presence of Sarcobatus to at least the latest glacial in Arizona, Colorado, New Mexico, and Utah (Betancourt 1990). Early Holocene records of Sarcobatus have been reported from western Montana (Mack et al. 1983) and northeastern Wyoming (Markgraf and Lennon 1986). However, suitable sites for the preservation of Pleistocene pollen are few in the northern Great Plains (Ritchie 1987), resulting in a scarcity of information concerning Montana and the Dakotas, while Alberta and Saskatchewan were unavailable for occupation insofar as they were covered by the Laurentide ice sheet. Nevertheless, fossil evidence on the whole suggests that the range of occurrence of Sarcobatus was relatively little altered during glaciation.

It seems likely on ecological grounds, however, that the species S. vermiculatus, at least, was edaphically confined during the Pleistocene. In addition to saline geological strata, large evaporationally saline areas, such as the beds of desiccated Pleistocene lakes, have existed since early Holocene and presently form important habitats for S. vermiculatus. Most of these sites were nonsaline or submerged during times of glaciation. However, outcrops of saline geologic strata, which are particularly common in the Colorado Plateau and northwestern Great Plains, must have formed an acceptable habitat for Sarcobatus in the Pleistocene, much as they do at present.

Sarcobatus apparently persisted in the Great Basin and other areas through the climatic changes of the glacial/interglacial cycles of the Pleistocene. In the Great Basin during the last glacial maximum (ca 18,000 yr B.P.), trees and shrubs of the modern pinyon-juniper woodland of the Great Basin were forced well to the south, and bristlecone and limber pines grew 1000 m or more below their current limits, suggesting that temperatures were much cooler than today (perhaps 8–10°C for summer months; Thompson 1990). Sarcobatus and other halophytes apparently weathered these changes in climate and survived until the present in essentially the same locations they have apparently lived for many millennia.

Adaptive Advantages of Polyploidy

The absence of tetraploid S. vermiculatus within the Great Basin or other parts of the central species range (Fig. 1) might suggest that the tetraploid race in these areas has been replaced by competition from octoploids. In several other apparently autoploid complexes, polyploid members of the complex are more widespread than diploids (Manton 1934, Zohary and Nur 1959, Stutz et al. 1975, Stutz 1983), which is commonly true in other sorts of polyploid complexes as well (Babcock and Stebbins 1938, Stebbins 1950). The competitive superiority observed in polyploids may arise in part because of the effects of one-way introgression and multiple origin (Zohary and Nur 1959, Stebbins 1971, Soltis et al. 1993), both of which act to widen the genetic base and ecological amplitude of polyploids. Our morphological and flavonoid data suggest significant amounts of genetic variation existing within octoploid S. vermiculatus and 12-ploid S. baleyi that may have contributed to their adaptive success.

Mechanism of Chromosome Number Increase

Endosperm balance number and "triploid block" refer to a mechanism limiting the occurrence of polyploidy, to a greater or lesser degree, within various angiosperm taxa (Woodell and Valentine 1961, Johnston et al. 1980). In those where it is strongly operative, triploids (which could be derived from an unreduced gamete plus a normal gamete) are unable to survive through embryo development. Polyploidization, if any, must then follow other less favorable pathways, such as somatic doubling or the union of simultaneous unreduced gametes. Since the primary nutritive tissue within the Caryophyllales seed is perisperm (of nucellar origin) rather than endosperm (Cronquist 1988), limitation of polyploidy by endosperm balance is probably not to be expected within this order. Absence of restraint of polyploidization by the endosperm balance mechanism might thus be an additional reason for polyploidy prevalence within species of this group.

Our data on Sarcobatus suggest an absence of endosperm balance effects and the function of the single-unreduced gamete pathway. Octoploid populations contain rare 12-ploid individuals, probably derived by unreduced gametes.
(4x + 8x = 12x) and apparent backcrosses of such to the parental chromosome number. Given sufficient selective value, a 12-ploid race like that of *S. bailey* might be expected to eventually appear in *S. vermiculatus*.

Since the tetraploid chromosomal race should give rise to hexaploid plants by unreduced gametes in the same manner, the existence of an octoploid chromosomal race in the absence of any hexaploid race is therefore unexpected. This anomaly could be best explained if the tetraploid race were relatively old and had therefore become diploidized. In that case hexaploid individuals that might be formed would be functionally equivalent to triploids, and sterile. Therefore, if a race of higher ploidy was produced, it would have to be at the octoploid level or higher, as is observed.

Similar reasoning could be applied to polyploids in other taxa, for instance *Atriplex canescens* and *A. confertifolia* (x = 9) of the Chenopodiaceae. Both taxa exhibit widespread tetraploid races (Stutz and Sanderson 1979, 1983, Sanderson et al. 1990, Sanderson and Stutz 1994) and have formed polyploids at hexaploid or octoploid levels, which would provide an indication of whether the respective tetraploids are diploidized or not. In *S. vermiculatus* the absence of diploids and the failure of the tetraploid race to polyploidize to the hexaploid level both suggest that the tetraploid race is ancient, probably dating back into the Pleistocene.

Success of octoploid *S. vermiculatus* in the relatively southern parts of the species range, in comparison to tetraploid populations located along the U.S.—Canada border and in northwestern California, may suggest that octoploids are better adapted to warm, arid climates. If this is the case, their ascendency over the tetraploids may therefore likely have occurred during the Holocene. The Sonoran tetraploid race occurs in a warmer climate, but it appears to be ecologically divergent and somewhat independent from the evolutionary trends of the remainder of the species.

**ACKNOWLEDGMENTS**

This research was supported by BHP-Minerals Inc. and Rocky Mountain Research Station, Forest Service, U.S. Department of Agriculture. The use of trade or firm names in this paper does not imply endorsement by the U.S. Department of Agriculture of any product or service.

We wish to thank those who have given encouragement or suggestions relating to this study.

**LITERATURE CITED**


to endosperm development in interspecific crosses. Theoretical and Applied Genetics 57:5-9.


Received 23 January 1998
Accepted 26 October 1998
### Sarcobatus Chromosome Races

**APPENDIX.** Chromosome count localities for *Sarcobatus baileyi* and *S. verrniculatus*. Counts not showing a date for meiotic bud collection were made from root tips.

<table>
<thead>
<tr>
<th>Ploidy</th>
<th>Plants counted</th>
<th>Nation, state, county: location</th>
<th>Date of meiotic bud collection</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Sarcobatus baileyi</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12x</td>
<td>USA, NV, Churchill Co.: mi 48, US 50, 1 mi E of Sand Mountain turnoff</td>
<td>11 APR 96</td>
<td></td>
</tr>
<tr>
<td>12x</td>
<td>USA, NV, Churchill Co.: mi 76, US 50, due NW of Eastgate</td>
<td>11 APR 96</td>
<td></td>
</tr>
<tr>
<td>12x</td>
<td>USA, NV, Esmeralda Co.: county line, US 95, S side of Tonoopa</td>
<td>15 APR 92</td>
<td></td>
</tr>
<tr>
<td>12x</td>
<td>USA, NV, Lander Co.: mi 1, NV 376, Big Smokey Valley, 15 mi S of US 50</td>
<td>15 APR 92</td>
<td></td>
</tr>
<tr>
<td>12x</td>
<td>USA, NV, Lander Co.: mi 11, NV 376, Big Smokey Valley</td>
<td>25 APR 95</td>
<td></td>
</tr>
<tr>
<td>12x</td>
<td>USA, NV, Lyon Co.: mi 11, NV 208, 5 mi E of Smith</td>
<td>12 APR 96</td>
<td></td>
</tr>
<tr>
<td>12x</td>
<td>USA, NV, Lyon Co.: mi 27, 15 mi N of Yerington</td>
<td>12 APR 96</td>
<td></td>
</tr>
<tr>
<td>12x</td>
<td>USA, NV, Lyon Co.: S side of Silver Springs</td>
<td>12 APR 96</td>
<td></td>
</tr>
<tr>
<td>12x</td>
<td>USA, NV, Mineral Co.: 5 mi S of Mina</td>
<td>24 APR 86</td>
<td></td>
</tr>
<tr>
<td>12x</td>
<td>USA, NV, Nye Co.: 5 mi N of Queen City Summit, NV 375</td>
<td>14 APR 92</td>
<td></td>
</tr>
<tr>
<td>12x</td>
<td>USA, NV, Nye Co.: mi 17, NV 379, S of Duckwater</td>
<td>11 MAY 88</td>
<td></td>
</tr>
<tr>
<td>12x</td>
<td>USA, NV, Nye Co.: NV 267-US 95 jet, Scotty's Junction</td>
<td>9 MAR 95</td>
<td></td>
</tr>
<tr>
<td>12x</td>
<td>USA, NV, Pershing Co.: 10 mi W of Sulphur</td>
<td>11 APR 91</td>
<td></td>
</tr>
<tr>
<td>12x</td>
<td>USA, NV, Pershing Co.: Toulon exit, I-80, 10 mi S of Lovelock</td>
<td>12 APR 96</td>
<td></td>
</tr>
<tr>
<td>12x</td>
<td>USA, NV, Washoe Co.: S-S ranch turnoff, N side of Wadsworth</td>
<td>12 APR 96</td>
<td></td>
</tr>
</tbody>
</table>

| **Sarcobatus verrniculatus** | | | |
| 4x | CAN, ALTA: 1.5 mi N of Warner | 21 JUN 89, 29 JUN 91 |
| 4x | CAN, ALTA: 1 mi N of Aden | 4 JUL 89 |
| 4x | CAN, ALTA: 2 mi E of Milk River | 29 JUN 91 |
| 4x | CAN, ALTA: 5 mi N of Milk River | 29 JUN 91 |
| 4x | CAN, ALTA: Dinosaur Provincial Park | 5 JUL 83 |
| 4x | CAN, ALTA: N bank of South Saskatchewan River, Suffield Mill. Res. | |
| 4x | CAN, ALTA: Orion | JUL 85, 4 JUL 89 |
| 4x | CAN, ALTA: Pendant Orielle | 4 JUL 89 |
| 4x | CAN, ALTA: Red Deer River coulee, N of Patricia | 18 AUG 96 |
| 4x | CAN, ALTA: S of 41A jet on Prov. hwy 41, 5 mi E of Medicine Hat | 1 AUG 85 |
| 4x | CAN, ALTA: Sandy Point | |
| 4x | CAN, ALTA: South Saskatchewan River, town of Bow River | 5 JUL 83 |
| 4x | CAN, SASK: 1 km E of Meleval, Prov. hwy 13 | 26 JUN 96 |
| 4x | CAN, SASK: Big Muddy Valley, S of Bengough | 27 JUL 96 |
| 4x | CAN, SASK: Cypress Lake, Prov. hwy 21 | 5 JUL 89, 1 AUG 95 |
| 4x | CAN, SASK: W Penteix access, Prov. hwy 13 | 26 JUN 96 |
| 4x | MEX, SON: RR km 193, 50 km W of Puerto Peñasco | 7 SEP 92 |
| 4x | MEX, SON: RR km 222, 20 km W of Puerto Peñasco | 13 SEP 95 |
| 8x | USA, AZ, Apache Co.: Many Farms | 22 JUL 84 |
| 8x | USA, AZ, Coconino Co.: Fredonia | 26 MAY 95 |
| 8x | USA, AZ, Maricopa Co.: Riggs Rd (Beltline) & 16th, 10 mi S of Phoenix | 25 AUG 93 |
| 8x | USA, AZ, Navajo Co.: Holbrook | 9 JUN 95 |
| 8x | USA, AZ, Pinal Co.: mi 140, AZ 287, 10 mi NW of Coolidge | 13 SEP 95 |
| 8x | USA, CA, Inyo Co.: 10 mi NW of Bishop | 18 AUG 94 |
| 8x | USA, CA, Inyo Co.: Big Pine | 18 AUG 94 |
| 8x | USA, CA, Inyo Co.: Deep Springs Valley | 18 AUG 94 |
| 8x | USA, CA, Lassen Co.: mi 13, 0.5 mi SW of Bieber | 17 AUG 94, 9 JUN 95 |
| 8x | USA, CA, Lassen Co.: mi 89, US 395, 20 mi N of Litchfield | 16 AUG 94 |
| 8x | USA, CA, Lassen Co.: Standish | 16 AUG 94 |
| 8x | USA, CA, Modoc Co.: 0.5 mi W of Likely | 16 AUG 94 |
| 8x | USA, CA, Modoc Co.: 2 mi W of Davis Creek | 17 AUG 94, 5 AUG 95 |
| 8x | USA, CA, Modoc Co.: 2 mi W of Davis Creek | 17 AUG 94, 9 JUN 95 |
| 8x | USA, CA, Modoc Co.: 7 mi W of Alturas | 9 JUN 95 |
| 8x | USA, CA, Modoc Co.: Canby | 17 JUL 94 |
| 8x | USA, CA, Modoc Co.: Centerville rd, 5 mi E of Canby | 17 AUG 94 |
| 8x | USA, CA, Modoc Co.: E side of Alkali Lake, CA 299, Cedarville | 17 JUL 94 |
| 8x | USA, CA, Modoc Co.: mi 13.75, US 395, 2 mi S of Alturas | 10 JUN 95 |
| 8x | USA, CA, Modoc Co.: Modoc Wildlife Refuge, US 395, 5 mi S of Alturas | 16 AUG 94 |
| 8x | USA, CA, Mono Co.: Bridgeport | 18 AUG 94 |
| 8x | USA, CA, Mono Co.: N side of Mono Lake, CA 167 | 18 AUG 94 |
| 8x | USA, CA, Mono Co.: S of Benton | 27 JUL 84 |
| 8x | USA, CA, Siskiyou Co.: 0.5 mi E of CA 161, US 97 jet, 3 mi NE of Dorris | 17 JUL 94 |
| 8x | USA, CA, Siskiyou Co.: 3 mi S of Granada | 9 JUN 95 |
12x (1) USA, NM, Torrance Co.: Laguna del Perro, 5 mi E of Willard 9 MAY 96
8x (1) USA, NM, Valencia Co.: Grants 26 MAY 95
8x (3) USA, NM, Valencia Co.: Laguna 26 MAY 95
8x (1) USA, NV, Churchill Co.: Middle Ledge 27 JUL 84
8x (2) USA, NV, Douglas Co.: mi 39, US 395, Carson Valley 5 AUG 95
8x (1) USA, NV, Elko Co.: 5 mi E of Carlin 23 JUN 82
8x (1) USA, NV, Elko Co.: 9 mi E of Montello 13 JUN 90
8x (2) USA, NV, Eureka Co.: 20 mi W of Eureka 11 MAY 89
8x (1) USA, NV, Eureka Co.: 8.5 mi W of NV 278, mi 40, 40 mi N of Eureka 15 AUG 94
8x (1) USA, NV, Eureka Co.: mi 45, NV 270, 40 mi S of Eureka (short stunted) 13 JUL 85
8x (2) USA, NV, Humboldt Co.: 16 mi W of Winnemucca, NV 49 15 JUN 85
8x (3) USA, NV, Humboldt Co.: Denio 17 JUL 94
8x (1) USA, NV, Humboldt Co.: OR state line, McDermitt 14 JUN 90
8x (1) USA, NV, Lander Co.: 10 mi W of Austin 10 MAY 89
8x (1) USA, NV, Lander Co.: Battle Mountain 30 MAY 86
8x (2) USA, NV, Lincoln Co.: Caliente 20 APR 89
8x (2) USA, NV, Lincoln Co.: Dry lake, 20 mi W of Caliente 27 JUN 86
8x (1) USA, NV, Lincoln Co.: Panaca 30 MAY 89
8x (1) USA, NV, Lincoln Co.: Rachel 6 AUG 85
8x (3) USA, NV, Lyon Co.: mi 11, NV 208, 5 mi E of Smith 9 JUL 82
8x (1) USA, NV, Mineral Co.: 15 mi E of Hawthorne 23 APR 88
8x (2) USA, NV, Nye Co.: 10 mi N of Beauty 9 JUL 82
8x (2) USA, NV, Nye Co.: 20 mi NE of Lone 16 JUN 80
ca. 12x (1) USA, NV, Nye Co.: 20 mi NW of Toopah towards Gabbs 21 APR 89
8x (1) USA, NV, Nye Co.: Gabbs 27 JUL 84
8x (2) USA, NV, Nye Co.: mi 103.5, 15 mi SW of Current 11 MAY 88
8x (3) USA, NV, Washoe Co.: Wadsworth 6 AUG 95
8x (2) USA, NV, White Pine Co.: Cherry Creek 16 MAY 85
ca. 9x (1) USA, NV, White Pine Co.: Cherry Creek 16 MAY 85
8x (1) USA, NV, White Pine Co.: US 6/50, Spring Valley 16 MAY 85
8x (2) USA, OR, Baker Co.: Baker 14 JUL 94
8x (3) USA, OR, Grant Co.: 1 mi E of Dayville 3 AUG 95
8x (5) USA, OR, Grant Co.: mi 119, OR 19, 20 mi NW of Dayville 2 SEP 94
8x (3) USA, OR, Grant Co.: mi 37, US 395, 1 mi S of Sylvis 4 AUG 95
8x (3) USA, OR, Harney Co.: 1 mi E of Burns, OR 78 4 AUG 95
8x (3) USA, OR, Harney Co.: Fields 18 JUL 94
8x (3) USA, OR, Jefferson Co.: Hay Creek, 2 mi S of Willowdale 16 JUL 94
8x (2) USA, OR, Klamath Co.: N side of Klamath Falls 17 JUL 94
8x (3) USA, OR, Lake Co.: Alkali Lake 17 JUL 94
8x (3) USA, OR, Lake Co.: mi 88, US 395, NE of Valley Falls 17 JUL 94
4x (3) USA, OR, Lake Co.: OR 140, W side of Lakeview 4 AUG 95
8x (3) USA, OR, Lake Co.: Plush 17 JUL 94
8x (3) USA, OR, Malheur Co.: 5 mi W of Vale 19 MAY 92
8x (1) USA, OR, Malheur Co.: Owylee River Canyon, 5 mi W of Adrian 13 SEP 94
8x (3) USA, OR, Malheur Co.: Rome 18 JUL 94
8x (1) USA, OR, Morrow Co.: 1 mi SE of Lexington 1 SEP 94
8x (3) USA, OR, Morrow Co.: 0.5 mi NE of Buggs (large stunted) 3 AUG 95
8x (2) USA, OR, Umatilla Co.: 2 mi W of Stanfield 14 JUL 94
8x (2) USA, OR, Union Co.: Ladd Refugio, US 30, La Grande 14 JUL 94
8x (3) USA, OR, Wheeler Co.: 0.5 mi E of OR 207–OR 19 Jet E of Spray 3 AUG 95
8x (2) USA, SD, Fall River Co.: Hat Creek, near Ardmore 6 JUN 89
8x (1) USA, SD, Lyman Co.: Cedar Creek, mi 146, SD 1806, 25 mi SE of Ft. Pierre 24 JUL 96
8x (1) USA, SD, Lyman Co.: Lower Brule 7 JUL 94
8x (1) USA, SD, Pennington Co.: 10 mi S of Wall 6 JUN 89
8x (1) USA, SD, Pennington Co.: SD 40, 0.5 mi S of Cheyenne River 29 JUL 95
8x (9) USA, UT, Duchesne Co.: Fruitland 10 JUL 95
8x (1) USA, UT, Emery Co.: US 6 exit, 1–70, 5 mi W of Green River 11 MAY 84
8x (1) USA, UT, Emery Co.: 5 mi N of Woodside 23 JUL 85
8x (2) USA, UT, Emery Co.: Islander Wash 6 JUN 89
6x (1) USA, UT, Emery Co.: Islander Wash (mistake, broken cells?) 2 MAY 85
8x (1) USA, UT, Grand Co.: 1 mi E of Green River 2 MAY 85
8x (2) USA, UT, Grand Co.: 20 mi N of Moab 26 JUN 86
8x (1) USA, UT, Iron Co.: 3 mi S of Parowan 26 JUN 86
8x (2) USA, UT, Iron Co.: 5 mi N of Beryl Junction (short stunted) 26 JUN 84
8x (3) USA, UT, Iron Co.: Lund (short stunted) 26 JUN 84
8x (1) USA, UT, Juab Co.: 5 mi NE of Scipio 26 JUN 86
8x (1) USA, UT, Millard Co.: 13 mi S of Deseret 30 MAY 89
8x (1) USA, UT, Millard Co.: 25 mi N of Milford (short statured) 30 MAY 89
8x (2) USA, UT, Millard Co.: USDA-FS Desert Exp. Sta., Pine Valley 24 MAY 94
8x (3) USA, UT, Rich Co.: mi 7, UT 16, 1 mi E of Woodruff 27 JUN 95
8x (1) USA, UT, San Juan Co.: 10 mi N of Hatch Trading Post 29 JUL 82
8x (1) USA, UT, San Juan Co.: mi 2, UT 262, 15 mi S of Blanding 12 MAY 84
8x (3) USA, UT, San Juan Co.: mi 82.5, US 191, 10 mi N of Monticello (large statured) 10 MAY 96
8x (2) USA, UT, Sevier Co.: 10 mi S of Fremont, UT 12 JUL 84
8x (1) USA, UT, Sevier Co.: 5 mi W of Joseph 17 JUN 82
8x (1) USA, UT, Tooele Co.: town of Rush Valley 29 JUN 83
8x (1) USA, UT, Tooele Co.: mi 51, I-80, E of Knolls 17 MAY 85
8x (1) USA, UT, Tooele Co.: Faust turnoff, mi 33, UT 36 17 MAY 85
8x (3) USA, WA, Douglas Co., WA 17-174 jct, 20 mi W of Grand Coulee 15 JUL 94
8x (3) USA, WA, Grant Co.: Moses Lake, Stratford rd, NE of airport 16 JUL 94
8x (2) USA, WA, Grant Co.: Soap Lake 15 JUL 94
8x (3) USA, WA, Lincoln Co.: 3 mi SW of Sprague on Sprague Lake rd 3 AUG 95
8x (2) USA, WA, Lincoln Co.: mi 103, WA 85, Lamona 16 JUL 94
8x (2) USA, WA, Walla Walla Co.: Touchet 14 JUL 94
8x (3) USA, WA, Walla Walla Co.: Walla Walla 3 AUG 95
8x (2) USA, WA, Yakima Co.: Granger 16 JUL 94
8x (1) USA, WA, Yakima Co.: WA 24-241 jct, near Hanford Reserve 16 JUL 94
8x (3) USA, WY, Big Horn Co.: N side of Greybull 28 JUL 95
8x (1) USA, WY, Carbon Co.: 13 mi S of Laramont 20 JUL 97
8x (2) USA, WY, Carbon Co.: 3 mi E of Rawlins 20 JUL 87
8x (1) USA, WY, Carbon Co.: Co. rd 402 exit, I-80, Elk Mtn. 20 JUL 87
8x (3) USA, WY, Carbon Co.: Saratoga 28 JUL 95
8x (1) USA, WY, Fremont Co.: Ice Slough, US 287, 15 mi W of J effery City 28 JUL 95
8x (3) USA, WY, Fremont Co.: Sweetwater Station 28 JUL 95
8x (3) USA, WY, Johnson Co.: exit 73, I-90, Crazy Woman Creek 29 JUL 95
8x (1) USA, WY, Lincoln Co.: Fontenelle Dam 17 JUN 88
8x (1) USA, WY, Lincoln Co.: Sage 18 JUN 93
8x (1) USA, WY, Natrona Co.: 5 mi N of Alcova 17 JUL 93
4x (1) USA, WY, Natrona Co.: Alcova (mistake, from broken cells?) 18 JUL 93
ca. 9x (1) USA, WY, Sublette Co.: 8 mi S of Boulder 3 JUL 95
8x (1) USA, WY, Sublette Co.: Pinedale 2 JUL 85
8x (1) USA, WY, Sweetwater Co.: 7 mi N of Rock Springs, US 187 19 JUN 80
8x (1) USA, WY, Sweetwater Co.: Sarson 2 JUL 85
8x (2) USA, WY, Sweetwater Co.: Red Desert 27 JUL 85
8x (1) USA, WY, Sweetwater Co.: Bock Springs 2 JUL 85
8x (3) USA, WY, Washakie Co.: county line, 15 mi SW of Worland 28 JUL 95